

Standardized Nomenclature for the Costal Wing Spots of the Genus *Anopheles* and Other Spotted-Wing Mosquitoes (Diptera: Culicidae)

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ABSTRACT A standardized nomenclature for the costal wing scale spots of species of the genus *Anopheles* and other spotted-wing mosquitoes is proposed. Emphasis is placed on species of *An. (Anopheles)*, Arribalzagia Series, which have three unique costal regions: the sector pale, the subcostal area, and the preapical pale. An isolated dark spot (the subcostal dark) distal to the sector dark spot at the end of the subcostal vein serves to define the series. The sector pale and accessory sector pale spots are defined in relation to the subcostal (sc-r) and radial (r_1 – r_5) crossveins, and the preapical pale and apical pale spots are defined in relation to the end of vein R_1 . These morphological markers, along with the humeral crossvein and the end of the subcostal vein, are used to establish reference points for the definition of the other costal spots. The significance of these spots in the classification of the genus *Anopheles* is discussed. Wing spots are illustrated for species of *An. (Anopheles)* Arribalzagia Series, *An. (Cellia)*, *An. (Lophopodomyia)*, *An. (Kerteszia)*, *An. (Anopheles)*, *An. (Nyssorhynchus)*, *Orthopodomyia*, *Aedeomyia*, *Culex*, and *Aedes (Finlaya)* Kochi Group.

KEY WORDS Insecta, Culicidae, *Anopheles*, wing spot nomenclature

MOSQUITO TAXONOMISTS always have used the regular areas of pale and dark scales on the wings of *Anopheles* mosquitoes for classification, descriptions, and keys. In an effort to name the costal wing scale spots of species of the *Anopheles (Anopheles)* Arribalzagia Series, we found that there were almost as many systems of nomenclature as there were publications on the subject (Table 1). It was difficult to recognize unique, homoplasious (Wiley 1981), or homologous spots because these systems for the most part were not based on morphological markers. Examination of many mosquito species revealed morphological features of significance that had been overlooked. These features enabled us to propose standardized names for the costal wing spots based on fixed morphological markers that can be applied not only to species of the Arribalzagia Series but to all of the spotted-wing anophelines and most other uniformly spotted-wing culicines.

We did not review all the available literature referring to costal wing spots, but several papers merit discussion because they contain elements that are part of the synthesis presented here. The only systematic effort to identify wing spots in anophelines was made by Christophers (1913). He identified various "nodal points" and spots or pigment centers, most of which are still recognized. It is difficult to determine an historical origin for all the

costal wing spot names, but it appears that Gater (1935) was probably the first to use terms similar to those employed here. Harrison (1980), Harrison & Scanlon (1975), and Reid (1968) also presented similar sets of names. Although Belkin (1962) was cited in Harbach & Knight (1980), his figure (p. 235) and accompanying explanation (p. 551) seemed to refer to species of the *Aedes (Finlaya)* Kochi Group and not specifically to the genus *Anopheles*. The names of costal spots used by Belkin probably were taken from Marks' (1947) treatment of the Kochi Group, which in turn cites Lee & Woodhill's (1944) work on the genus *Anopheles*. Our work is based on the summary of Harbach & Knight (1980), who gave definitions and synonyms for the spots and cited some of the authors presented in Table 1. Their definitions were clear but deficient in that nearly all the spots were defined in relation to each other. We accept the terms used by Harbach & Knight (1980), because they make logical reference to the location of spots on the wing.

Names for costal wing scale spots in anophelines have been based on species of the subgenus *Cellia* because many members of the subgenus have the maximum number of spots. It has been assumed that all the other anophelines exhibit a reduction. Exceptions were Christophers (1913), who attempted to classify all groups of anophelines; Faran (1980), who illustrated a species of *An. (Nyssorhynchus)*; and Zavortink (1973), who illustrated a species of *An. (Kerteszia)*. The names used by the latter two authors were inconsistent with the names of spots as interpreted by others. Although many species of the subgenus *Cellia* have the maximum

The views of the authors do not purport to reflect the views of the supporting agency.

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Table 1. Comparison of selected systems for naming pale and dark costal wing spots in genus *Anopheles*

Proposed nomenclature	Christophers 1913	Root 1926	King 1932	Christophers 1933	Gater 1935	Russell et al. 1943
Basal pale	Not shown	B1	Not shown	Not shown	Not named	Not named
Basal dark	Basal acc. spot (in part)	Not named	Inner acc. dark spot (in part)	Inner prehumeral dark acc. spot	Inner prehumeral dark acc. spot ^a	Not shown
Prehumeral pale	Not shown	Not shown	Not shown	Prehumeral pale interr.	Prehumeral pale interr.	H1
Prehumeral dark	Basal acc. spot (in part)	Not named	Inner acc. dark spot (in part)	Outer prehumeral dark acc. spot	Outer prehumeral dark acc. spot ^a	Not named
Humeral pale	Humeral nodal point	B2	White interr. basal 1/3 of costa	Humeral pale interr.	Humeral pale	H2
Humeral dark	Basal acc. pigment area	Not named	Outer acc. dark spot	Humeral dark acc. spot	Humeral dark acc. spot	Not named
Presector pale	Inner pale spot	B3	Presector white spot	Presector pale area	Presector pale area	H3
Presector dark	Inner main costal spot center	Not named	Presector dark spot	Presector dark spot	Presector dark spot	Basal dark spot
Sector pale	Sector nodal point	M1	Sector spot	Sector pale area	Sector pale area	Sectoral spot
Sector dark	Middle main costal spot center	Not named	Midcostal spot	Middle dark spot	Middle dark spot	Median dark spot
Acc. sector pale	Acc. sector nodal point	M2 and M3	Acc. sector spot	Acc. sector pale area	Acc. sector pale area	Acc. sector spot
Subcostal pale	Subcostal nodal point	Sc	Subcostal white spot	Subcostal pale area	Subcostal pale area	Subcostal spot
Preapical dark	Subapical main costal spot center	Not named	Subapical dark spot	Preapical dark spot	Preapical dark spot	Preapical dark spot
Preapical pale	"C.I"	Apical pale (in part)	Subapical white spot	Preapical pale area	Preapical pale area	Preapical spot
Apical dark	Apical main costal spot center	Not named	Apical dark spot	Apical dark spot	Apical dark spot	Apical dark spot
Apical pale	Apical nodal point	Apical pale (in part)	Apical white spot	Apical pale area	Apical pale area	Apical spot

^a Undivided, prehumeral dark accessory spot.
^b "c" is pale interruption of third dark area of first vein.
^c Also contains accessory R₁ pale on R₁.
^d When absent, forms the subbasal dark.

number of spots, a potential problem lies in the tacit assumption that the genus *Anopheles* is monophyletic, and therefore the wing spots of all anopheline subgenera are homologous. We will not treat phylogenetic questions directly, but we will present evidence which supports the present classification and suggests further research to improve this classification system. We hope that our observations will be a source of new taxonomic characters. Correspondence of the costal wing spots and morphological markers of anophelines with other culicines was an unexpected discovery that enabled us to provide functional definitions of the spots in those few spotted-wing species in the genera *Aedes*, *Aedeomyia*, *Culex*, *Orthopodomyia*, *Psorophora*, and *Uranotaenia*.

Materials and Methods

We examined all species of the genus *Anopheles* with either unicolorous or dark and pale-spotted

wings and most other culicines with dark and pale-spotted wings in the collection of the National Museum of Natural History. In most cases, one to three examples of each species were studied. We did not study the pigmented areas (spots) on the wing membrane itself. Pigment areas are present in species of the Arribalzagia Series and other anophelines (Christophers 1913) and are known to be of some taxonomic value in at least some species of the genera *Aedes* and *Culiseta*. Christophers (1913) attempted to name most of the pale and dark scale spots on the posterior veins. Some of the spots are associated with fixed morphological markers at the ends of crossveins, the furcation of veins, and the ends of veins at the wing margin usually associated with distinct pale or dark fringe spots. These spots have some taxonomic value and are adequately described using their morphological positions as defined in Harbach & Knight (1980). The terms "spot," "mark," "interruption," and "area" have been used to describe pale and dark scale patches

Table 1. Continued

Reid 1968	Gillies & de Meillon 1968	Zavortink 1973	Harrison & Scanlon 1975	Faran 1980	Harrison 1980	Harbach & Knight 1980
Not named	Not shown	Basal pale	Not shown	Basal pale?	Basal pale	Basal pale
Prehumeral dark mark (in part)	Not named	Basal dark (in part)	Inner prehu- meral acc. dark	Not shown	Basal dark	Basal dark
Prehumeral pale spot	Not shown	Not shown	Prehumeral pale	Basal pale	Prehumeral pale	Prehumeral pale
Prehumeral dark mark (in part)	Not named	Basal dark (in part)	Not named	Basal dark	Prehumeral dark	Prehumeral dark
Humeral pale spot	"a," humeral pale mark- ing	Humeral pale	Humeral pale	Humeral pale	Humeral pale	Humeral pale
Humeral dark mark	Not named	Humeral dark (in part)	Humeral dark	Subbasal dark	Humeral dark	Humeral dark
Presector pale spot	"a," presector pale	Not shown	Presector pale	Subbasal pale	Presector pale	Presector pale ^d
Presector dark mark	"A"	Humeral dark (in part)	Presector dark	Presectoral dark	Presector dark	Presector dark
Sector pale spot	"b," sector spot	Presectoral pale	Sector pale	Presectoral pale	Sector pale	Sector pale
Middle dark mark	"B"	Presect. dark (in part) sec- toral dark (in part)	Middle dark	Sectoral dark (in part) subcostal dark (in part)	Sector dark	Median dark
Acc. sector pale spot	"b," acc. sector pale spot	Sectoral pale	Acc. sector pale	Sectoral pale	Acc. sector pale	Acc. sector pale
Subcostal pale spot	"c," subcostal spot	Subcostal pale	Subcostal pale	Subcostal pale	Subcostal pale	Subcostal pale
Preapical dark mark	"C" ^b	Preapical dark	Preapical dark	Preapical dark	Preapical dark ^c	Preapical dark
Preapical pale spot	"d," subapical spot	Preapical pale	Preapical pale	Preapical pale	Preapical pale	Preapical pale
Apical dark mark	"D"	Not named	Apical dark	Apical dark	Apical dark	Apical dark
Apical pale spot	"e," apical spot	Not shown	Not named	Not shown	Apical pale	Apical pale

on the wing (Table 1). We follow Harbach & Knight (1980) and use "spot" to describe any dark or pale scale patch on the wing.

Species Examined. *Anopheles* (*Anopheles*) other than the Arribalzagia Series (103 species; an asterisk indicates unicolorous species); *aberrans* Harrison and Scanlon, *aikenii* James, *albotaeniat* (Theobald), *algeriensis* Theobald, *annulipalpis* Lynch Arribalzagia, *arboricola* Zavortink, *argyropus* (Swellengrebel), *asiaticus* Leicester, *atrati* Skuse, *atropos* Dyar and Knab, *aztecus* Hoffmann, *baezai* Gater, *bancroftii* Giles, *barberi* Coquillett, *barbirostris* Van der Wulp, *barbumbrosus* Strickland and Chowdhury, *barianensis* James, *bengalensis* Puri, *bradleyi* King, *brevipalpis* Roper, *campestris* Reid, *claviger* (Meigen), *colledgei* Marks, *collessi* Reid, *concolor* Edwards, *coustani* Laveran, *crawfordi* Reid, *crucians* Wiedemann, *culiciformis* Cogill, *donaldi* Reid, *earlei* Vargas, *eiseni* Coquillett, *fausti* Vargas, *fragilis* (Theobald), *franciscanus* McCracken, *franciscoi* Reid, *freeborni* Aitken, *fuscicolor* Van

Someren, *georgianus* King, *gigas* Giles, *grabhamii* Theobald, *habibi* Mulligan and Puri, *hectoris* Gaiquinto-Mira, *hodgkini* Reid, *hyrcanus* (Pallas), *implexus* (Theobald), *insulaeflorum* (Swellengrebel and Swellengrebel de Graaf), *interruptus* Puri, *judithae* Zavortink, *koreicus* Yamada and Watanabe, *labbranchiae* Falleroni, *lesteri* Baisas and Hu, *letifer* Sandosham, *lewisi* Ludlow, *lindesayi* Giles, *maculipennis* Meigen, *manalangi* Mendoza, *marteri* Senevet and Prunelle, *montanus* Stanton and Hacker, *namibiensis* Coetzee, *nigerimus* Giles, *nitidus* Harrison and Scanlon, *noniae* Reid, *obscurus* (Gruenberg), *occidentalis* Dyar and Knab, *palmaris* (Rodenwaldt), *paludis* Theobald, *papuensis* Dobrotworsky, *parapunctipennis* Martini, *peditaeniatus* (Leicester), *perplexens* Ludlow, *pilotum* Harrison and Scanlon, *plumbeus* Stephens, *pollicaris* Reid, *powderi* Zavortink, *pseudobarbirostris* Ludlow, *pseudopunctipennis* Theobald, *pullus* Yamada, *punctipennis* (Say), *pursati* Laveran, *quadrimaculatus* Say, *reidi* Harrison, *roperi* Reid, *sacharovi* Favre, *samarensis* Rozeboom,

saperoi Bohart and Ingram, *saperoi ohamai* Ohama, *separatus* (Leicester), *sinensis* Wiedemann, *sineroides* Yamada, **sintonoides* Ho, **stigmaticus* Skuse, *stricklandi* Reid, *symesi* Edwards, **tasmانيensis* Dobrotworsky, *tenebrosus* Doenitz, **tigertti* Scanlon and Peyton, *umbrosus* (Theobald), *vanus* Walker, **walkeri* Theobald, *wellingtonianus* Alcock, *whartoni* Reid, *xelajuensis* de Leon, *yatsushiroensis* Miyazaki, *ziemanni* Gruenberg.

Anopheles (*Anopheles*) Arribalzagia Series (22 species): *anchietai* Correa and Ramalho, *apicimacula* Dyar and Knab, *bonnei* Da Fonseca and Da Silva Ramos, *bustamentei* Galvao, *evandroi* Da Costa Lima, *fluminensis* Root, *gabaldoni* Vargas, *guarao* Anduze and Capdevielle, *intermedius* (Peryassu), *maculipes* (Theobald), *malefactor* Dyar and Knab, *mattogrossensis* Lutz and Neiva, *mediopunctatus* (Theobald), *minor* Da Costa Lima, *neomaculipalpus* Curry, *periyassui* Dyar and Knab, *pseudomaculipes* (Peryassu), *punctimacula* Dyar and Knab, *rachoui* Galvao, *shannoni* Davis, *veruslanei* Vargas, *vestitipennis* Dyar and Knab.

Anopheles (*Cellia*) (102 species): *aconitus* Doenitz, *amictus* Edwards, *annularis* Van der Wulp, *annulipes* Walker, *ardensis* (Theobald), *argenteolobatus* (Gough), *aurirostris* (Watson), *balabacensis* Baisas, *barberellus* Evans, *brunnipes* (Theobald), *christyi* (Newstead and Carter), *cinereus* Theobald, *clowi* Rozeboom and Knight, *confusus* Evans and Leeson, *cristatus* King and Baisas, *culicifacies* Giles, *cydippis* de Meillon, *demeilloni* Evans, *dirus* complex, *elegans* (James), *farauti* Laveiran, *filipinae* Manalang, *flavirostris* (Ludlow), *fluviatilis* James, *funestus* Giles, *gambiae* Giles, *garnhami* Edwards, *hackeri* Edwards, *hancocki* Edwards, *hargreavesi* Evans, *hispaniola* (Theobald), *indefinitus* (Ludlow), *introlatus* Colless, *jamesii* Theobald, *jeyporiensis* James, *karwari* (James), *kingi* Christophers, *kolambuganensis* Baisas, *kochi* Doenitz, *koliensis* Owen, *leesoni* Evans, *letabensis* Lambert and Coetzee, *leucosphyrus* Doenitz, *limosus* King, *listeri* de Meillon, *litoralis* King, *longipalpis* (Theobald), *longirostris* Brug, *ludlowae* (Theobald), *lungae* Belkin and Schlosser, *macarthuri* Colless, *machardyi* Edwards, *maculatus* Theobald, *majidi* Young and Majid, *malienensis* Bailly-Choumara and Adam, *mangyanus* (Banks), *melas* Theobald, *meraukens* Venhuis, *merus* Doenitz, *minus* Theobald, *moghulensis* Christophers, *moucheti* Evans, *multicolor* Cambouliu, *natalensis* (Hill and Haydon), *nataliae* Belkin, *nili* (Theobald), *nivipes* (Theobald), *novaguinensis* Venhuis, *pallidus* Theobald, *pampanai* Buettiker and Beales, *parangensis* (Ludlow), *pattoni* Christophers, *pharoensis* Theobald, *philippinensis* Ludlow, *pretoriensis* (Theobald), *pseudojamesi* Strickland and Chowdhury, *pulcherrimus* Theobald, *punctulatus* Doenitz, *radama* de Meillon, *rhodesiensis* Theobald, *riparis* King and Baisas, *rivulorum* Leeson, *ruarinus* Edwards, *rufipes* (Gough), *schwetzi* Evans, *sergentii* (Theobald),

smithii Theobald, *solomonis* Belkin, Knight, and Rozeboom, *splendidus* Koidzumi, *squamosus* Theobald, *stephensi* Liston, *subpictus* Grassi, *sulawesi* Waktoedi, *sundaicus* (Rodenwaldt), *superpictus* Grassi, *takasagoensis* Morishita, *tessellatus* Theobald, *theileri* Edwards, *theobaldi* Giles, *turkhudi* Liston, *vagus* Doenitz.

Anopheles (*Nyssorhynchus*) (15 species): *albimanus* Wiedemann, *albitarsis* Lynch Arribalzagia, *aquasalis* Curry, *argyritarsis* Robineau-Desvoidy, *benarrochi* Gabaldon, *braziliensis* (Chagas), *darlingi* Root, *evansae* (Brethes), *nuneztovari* Gabaldon, *oswaldoi* (Peryassu), *parvus* (Chagas), *rangeli* Gabaldon, Cova Garcia, and Lopez, *strodei* Root, *triannulatus* (Neiva and Pinto), *trinkae* Faran.

Anopheles (*Kerteszia*) (eight species): *bambusicolus* Komp, *bellator* Dyar and Knab, *boliviensis* (Theobald), *cruzei* Dyar and Knab, *homunculus* Komp, *laneanus* Correa and Cerqueira, *neivai* Howard, Dyar, and Knab, *pholidotus* Zavortink.

Anopheles (*Lophopodomomyia*) (four species): *gilesi* (Peryassu), *oiketorakras* Osorno-Mesa, *pseudotibiamaculatus* Galvao and Barretto, *squamifemur* Antunes.

Aedes (*Finlaya*) Kochi Group (12 species): *bougainvillensis* Marks, *burnetti* Belkin, *fijiensis* Marks, *franclemonti* Belkin, *freycinetiae* Laird, *hollingsheadi* Belkin, *knighti* Stone and Bohart, *kochi* (Doenitz), *neogeorgianus* Belkin, *oceanicus* Belkin, *samoanus* (Gruenberg), *schlosseri* Belkin.

Orthopodomomyia (nine species): *anopheloides* (Giles), *albipes* Leicester, *fascipes* (Coquillett), *flavicosta* Barraud, *flavithorax* Barraud, *lanyuensis* Lien, *madrensis* Baisas, *siamensis* Zavortink, *wilsoni* Macdonald.

Aedeomyia (*Aedeomyia*) (five species): *catasticta* Knab, *squamipennis* (Lynch Arribalzagia), *venustipes* (Skuse), *africana* Neveu-Lemaire, *pauliani* Grjebine.

Aedeomyia (*Lepiothauma*) (one species): *furfura* (Enderlein).

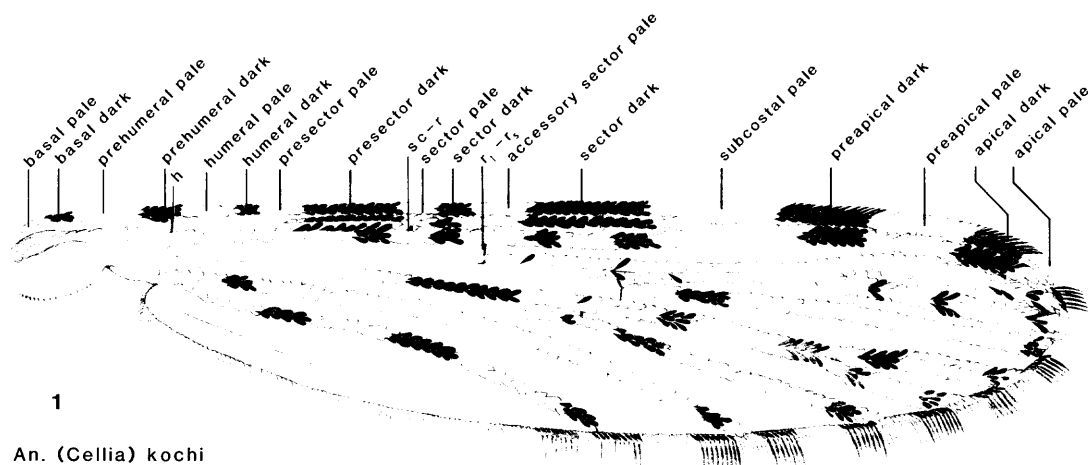
Culex (*Culex*) (six species): *mimeticus* Noe, *mimulus* Edwards, *murrelli* Lien, *orientalis* Edwards, *tsengi* Lien, *jacksoni* Edwards.

Culex (*Lutzia*) (two species): *allostigma* (Howard, Dyar, and Knab), *bigoti* Bellardi.

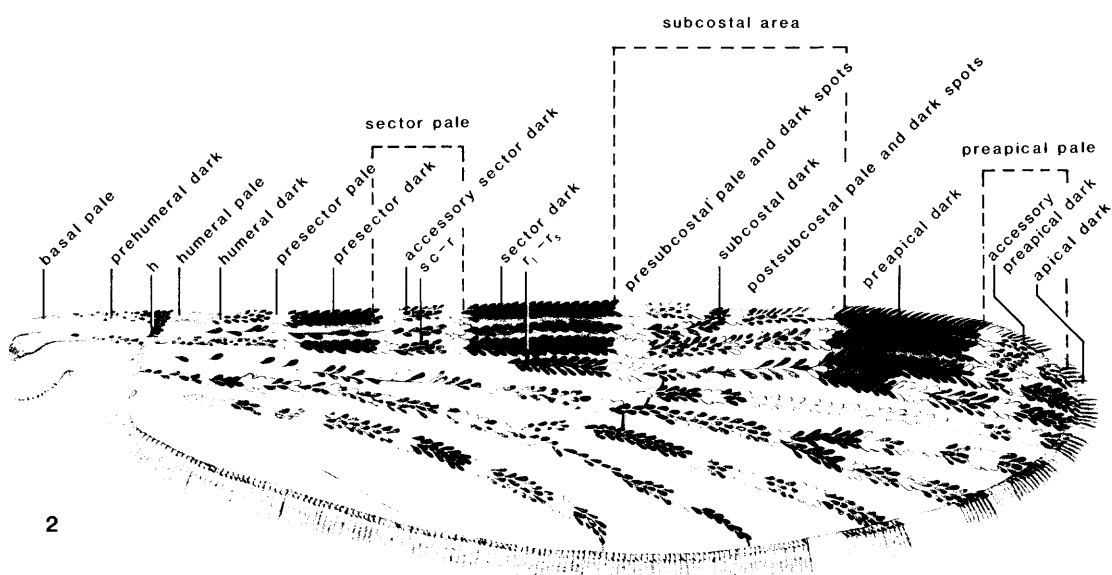
Psorophora (*Grahamia*) (one species): *signipennis* (Coquillett).

Uranotaenia (*Uranotaenia*) (three species): *bi-maculiala* Leicester, *edwardsi* Barraud, *micans* Leicester.

Abbreviations. The following are abbreviations used in the figures. An example of each can be found on the figure(s) given. Most follow Harbach & Knight 1980. The nine names for costal wing spots introduced here for the first time are marked with an asterisk (*); spots redefined or clarified are marked with two asterisks (**). **AD, apical dark spot (Fig. 1); **AP, apical pale spot (Fig. 1); *APD, accessory preapical dark spot (Arribalzagia Series) (Fig. 2); *ASD, accessory sector dark spot (Arribalzagia Series) (Fig. 2); **ASP, accessory sector



An. (Cellia) kochi



An. (Anopheles) Arribalzagia Series

Fig. 1 and 2. Wings of female anophelines. (1) *An. (Cellia) kochi*, "Ledo, Assam, V.I. Miles—44," (2) *An. (Anopheles) malefactor*, "Panama GG 8."

pale spot (Fig. 1); BD, basal dark spot (Fig. 1); BP, basal pale spot (Fig. 1); C, costa (Figure 28); h, humeral crossvein (Fig. 1); HD, humeral dark spot (Fig. 1); HP, humeral pale spot (Fig. 1); **PD, preapical dark spot (Fig. 1); PHD, prehumeral dark spot (Fig. 1); PHP, prehumeral pale spot (Fig. 1); *POSCD, postsubcostal dark spot (Arribalzagia Series and *Orthopodomyia*) (Fig. 2 and 36); *POSCP, postsubcostal pale spot (Arribalzagia Series and *Orthopodomyia*) (Fig. 2 and 36); **PP, preapical pale spot (Fig. 1); *PRSCD, presubcostal dark spot (Arribalzagia Series) (Fig. 2); *PRSCP, presubcostal

pale spot (Arribalzagia Series) (Fig. 2); PSD, presector dark spot (Fig. 1); PSP, presector pale spot (Fig. 1); R, radius (Fig. 25); R₁, radius-one (Fig. 25 and 28); R₂, radius-two (Fig. 28); R₃, radius-three (Fig. 28); R_s, radial sector (Fig. 25); *SAD, subapical dark spot (preapical dark plus apical dark) (Fig. 29); SBD, subbasal dark spot (humeral dark spot plus presector dark spot) (Fig. 4); Sc, subcosta (Fig. 25 and 28); *SCA, subcostal area (Arribalzagia Series and *Orthopodomyia*) (Fig. 2); *SCD, subcostal dark spot (Arribalzagia Series) (Fig. 2); **SCP, subcostal pale

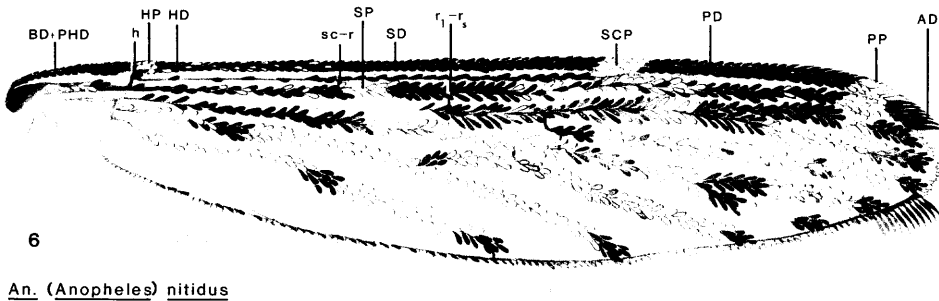
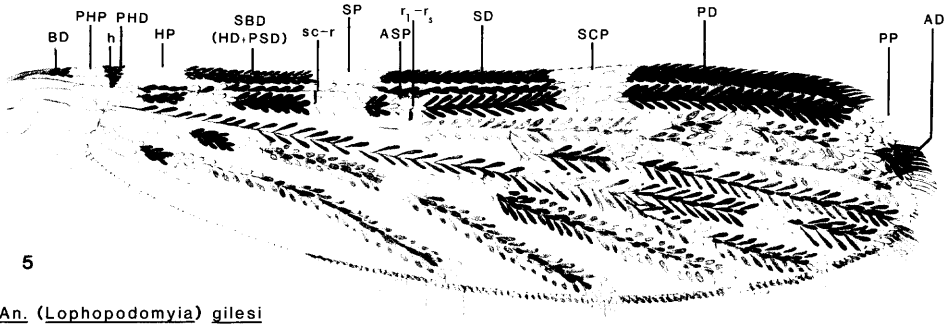
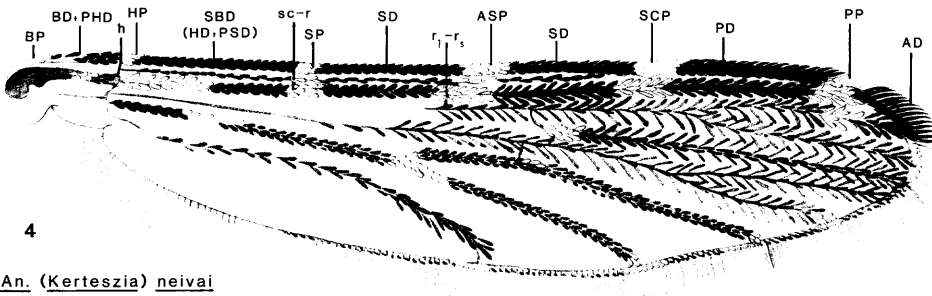
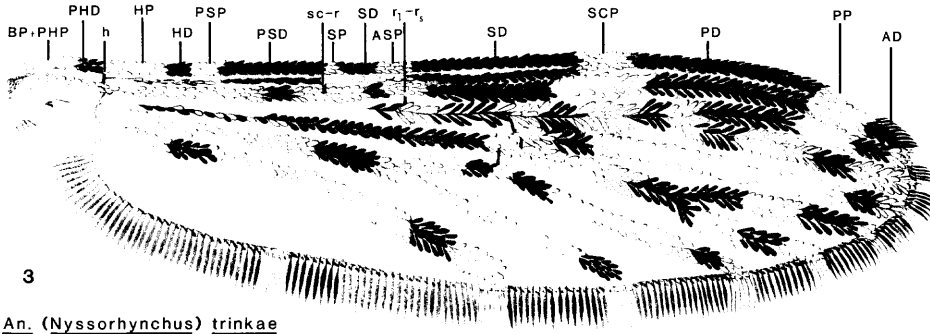


Fig. 3-6. Wings of female anophelines (see text for abbreviations). (3) *An. (Nyssorhynchus) trinkae*, Bolivia, Chapare, 12 Jan. 1982, (4) *An. (Kerteszia) neivai*, Canal Zone, Fort Randolph, (5) *An. (Lophopodomyia) gilesi*, Brazil, Minas Gerais, Rio Doce, 1946, (6) *An. (Anopheles) nitidus*, Vietnam, Phu Lam, PL 2994.

spot (Fig. 1); sc-r, subcostal crossvein (Fig. 1); SD, sector dark spot (Fig. 1); **SP, sector pale spot (Fig. 1).

Results and Discussion

The subgenus *Cellia* (Fig. 1) serves as the basis for most wing spot classification systems. The example used here, *An. (Cellia) kochi*, exhibits an accessory sector pale spot on veins R, Sc, and C. Table 1 compares the wing spot names accepted here with the interpretations of previous authors. Fig. 2 illustrates our proposed nomenclature for species of the Arribalzagia Series. Recognition by us of three unique areas (sector pale, subcostal, and preapical pale) on the wings of species of the Arribalzagia Series supports the classification of Reid & Knight (1961), who used the shape of the pupal trumpet as a definitive character for this New World group; it provides further evidence that the Arribalzagia Series is monophyletic.

Subcostal Pale Spot. This spot is defined by Harbach & Knight (1980, 54) as "the group of pale scales occurring on the costa and radius-one at and beyond the end of subcosta-one between the median dark and preapical dark." This definition is suitable for species of the subgenera *Cellia* (Fig. 1), *Nyssorhynchus* (Fig. 3), *Lophopodomomyia* (Fig. 5), and *Anopheles* (Fig. 6) but not for the Arribalzagia Series (Fig. 2). Species of the subgenus *Kerteszia* (Fig. 4) also differ slightly.

We found that in the Arribalzagia Series, the subcostal vein always ends in or at the distal end of an isolated dark spot distal to the sector dark spot (Fig. 7-24, distal-most arrow). The spot is a definitive character for this group. It was seen by others but not recognized for its value in classification. Christophers (1913) noted it for *An. maculipes* and *An. mediopunctatus*; Root (1927) for *An. fluminensis*; Christophers (1923) for *An. amazonicus* Christophers (= *An. mattogrossensis*); and Komp (1942) for *An. punctimacula*, *An. apicimacula*, and *An. neomaculipalpus* but not for *An. vestitipennis* or *An. mediopunctatus*. Reid & Knight (1961) came close to using this as a group character but instead said that the costa has two pale spots near the junction of the subcosta. Even though two pale spots define a dark spot, most species of the Arribalzagia Series have more than two pale spots in the area of the subcosta. Therefore, the constant character is the presence of the dark spot at the end of the subcosta with a variable number of pale and dark spots on either side of it. We name the spot at the end of the subcosta in species of the Arribalzagia Series (Fig. 2) the **subcostal dark spot** and those spots basal to it the **presubcostal pale and dark spots** and those distal to it the **postsubcostal pale and dark spots**. We name the area where these spots are found the **subcostal area**.

The fewest spots on each side of the subcostal dark is one (*An. mattogrossensis*). Most commonly,

there are two pale and one dark spot on each side (*An. intermedius*, *An. evandroi*, *An. apicimacula*, and other species), but *An. fluminensis* and *An. guarao* have three pale and two dark spots on each side. Other combinations of numbers of spots are evident, and we suspect that the size and number of these spots may provide useful species characters once intraspecific variation has been investigated. We have noted some variability in the subcostal area in our brief review of species of the Arribalzagia Series, therefore the illustrations (Fig. 7-24) should not be relied upon for species determinations.

The definition of Harbach & Knight (1980) for the subcostal pale spot does not always apply in species of the subgenus *Kerteszia* (Fig. 4) because the subcosta joins the costa in the sector dark or at its distal end. Intraspecific variation has not been investigated, but in the small number of specimens of each species examined, the position of the subcostal ending varies from the middle to the distal end of the sector dark spot.

Sector Pale and Accessory Sector Pale Spots. The sector pale spot is defined by Harbach & Knight (1980, 53) as "the group of pale scales occurring on the costa, subcosta and radius before the splitting of radius-one and the radial sector and between the presector dark and median dark." They also defined the accessory sector pale as "the group of pale scales sometimes occurring on the radius at or just distad of the splitting of radius-one and the radial sector and usually separated by a dark spot from the sector pale." The sector pale spot usually can be identified in species of the genus *Anopheles*, but in the Arribalzagia Series (Fig. 2), the pale spot corresponding to the sector pale bears a resemblance to the sector pale and accessory sector pale spots found in species such as *An. (Cellia) kochi* (Fig. 1).

To solve the problem caused by this similarity, we examined two crossveins. The first is a little-noticed crossvein found between the subcosta and radius (sc-r), perhaps first noted by Skuse (1889). It has had various names which are summarized in Table 2. Harbach & Knight (1980) do not illustrate it but define it as "the short crossveinlike posterior branch of the subcosta connected with the radius." Although historically sc-r has been considered a crossvein by mosquito workers, Harbach & Knight (1980) call it the second subcostal vein. Because it resembles other well-known crossveins in mosquitoes, we continue to refer to it as the subcostal (sc-r) crossvein.

We discovered that except for some species of the subgenus *Anopheles*, the sc-r crossvein is found in the sector pale spot. Root (1926) also associated this crossvein with a pale spot (M₁) in a few species of the subgenus *Nyssorhynchus*. We redefine the **sector pale spot** as the group of pale scales occurring on the costa, subcosta and/or radius associated with or just distad of the sc-r crossvein (Fig. 1 and 25).



7
An. (Anopheles) intermedius



8
An. (Anopheles) apicimacula



9
An. (Anopheles) evandroi



10
An. (Anopheles) rachoui



11
An. (Anopheles) mediopunctatus



12
An. (Anopheles) vestitipennis

Fig. 7-12. Wings of female anophelines (except *An. mediopunctatus*), of Arribalzagia Series. (7) *An. (Anopheles) intermedius*, Brazil, BRA 304, (8) *An. (Anopheles) apicimacula*, holotype, Guatemala, Livingston, (9) *An. (Anopheles) evandroi*, No. 3040, Inst. Osw. Cruz, (10) *An. (Anopheles) rachoui*, lectotype, Brazil, Baia, Sao Bento Lago, Sch. Pub. Hlth., Sao Paulo, (11) *An. (Anopheles) mediopunctatus*, holotype, Brazil, British Museum (NH), (12) *An. (Anopheles) vestitipennis*, lectotype, Guatemala, Alta V. Paz.

13

An. (Anopheles) maculipes

14

An. (Anopheles) punctimacula

15

An. (Anopheles) malefactor

16

An. (Anopheles) shannoni

17

An. (Anopheles) anchietai

18

An. (Anopheles) gabaldoni

Fig. 13-18. Wings of female anophelines of Arribalzagia Series. (13) An. (Anopheles) maculipes, holotype, Brazil, Sao Paulo, British Museum (NH), (14) An. (Anopheles) punctimacula, holotype, Panama, Canal Zone, and PA 1175-64, Panama, (15) An. (Anopheles) malefactor, lectotype, Panama, Rio Chagres, (16) An. (Anopheles) shannoni, paratype, Brazil, Para, (17) An. (Anopheles) anchietai, paratype, "15.852," Sch. Pub. Hlth., Sao Paulo, (18) An. (Anopheles) gabaldoni, Belice, BH 340.

19

An. (Anopheles) minor

20

An. (Anopheles) neomaculipalpus

21

An. (Anopheles) peryassui

22

An. (Anopheles) fluminensis

23

An. (Anopheles) guarao

24

An. (Anopheles) mattogrossensis

Fig. 19-24. Wings of female anophelines of Arribalzagia Series. (19) *An. (Anopheles) minor*, Brazil, Natal, Cajupiranga, (20) *An. (Anopheles) neomaculipalpus*, paratype?, "1271," Panama, Canal Zone, Mindi, VII-13, (21) *An. (Anopheles) peryassui*, paratype, 27747, (22) *An. (Anopheles) fluminensis*, "N. 842," locality not known, Sch. Pub. Hlth., Sao Paulo, (23) *An. (Anopheles) guarao*, Venezuela, Caripito, 110-2, X-10-44, (24) *An. (Anopheles) mattogrossensis*, Brazil, Para, Fordlandia, June 1931.

Table 2. Examples of interpretations of sc-r and r_1-r_s crossveins

Reference	sc-r	r_1-r_s
Skuse 1889	subbasal crossvein	?
Nuttall & Shipley 1901	not shown	cross nervure between R_1 and R_2
Theobald 1901	subcostal transverse	"x," marginal transverse
Blanchard 1905	"p," subcostal crossvein	"q," marginal crossvein
Christophers 1913	not shown	"c.v. 2"
Comstock 1918	Sc_2 , second subcostal	r, radial
Christophers & Barraud 1924	"c.v.," undescribed crossvein	r
Root 1926	not named	not named
Christophers 1933	not named	not named
Gater 1935	sc-r, subcosto-radial	r, radial
Snodgrass 1935	Sc_2 ?	r ?
Russell et al. 1943	not shown	not shown
Cova-Garcia 1961	sc, subcostal crossvein	r, radial or marginal crossvein
Belkin 1962	subcostal	not named
Reid 1968	not named	not named
Gillies & DeMeillon 1968	not shown	not named
Zavortink 1973	not shown	not named
Harrison & Scanlon 1975	not shown	not named
Faran 1980	not shown	not named
Harrison 1980	Sc-R	not named
Harbach & Knight 1980	Sc_2 , subcosta-two	not named

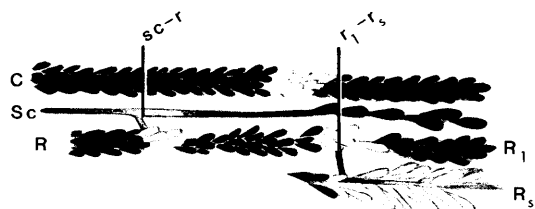
Species of the subgenera *Cellia*, *Nyssorhynchus*, *Lophopodomys*, and *Kerteszia* have sector pale spots in the area of the sc-r crossvein (Fig. 1, 3–5). In the Arribalzagia Series (Fig. 2, 7–24, basal-most arrow), the association of sc-r with the sector pale spot also is evident and establishes that the sector pale is present in this group.

Other members of the subgenus *Anopheles* (Fig. 6) also have a pale spot in the approximate location of the sc-r crossvein usually confined to R_s but its position varies from species to species. In most species, sc-r is in the proximal half of the spot; in others (e.g., *An. bariensis*, *An. crucians*, *An. eiseni*, *An. georgianus*, *An. franciscoi*, *An. nitidus*, *An. peditaeniatus*, *An. pursati*, *An. baezi*, and *An. albotaeniatus*), this pale spot is just distad of sc-r. Some species (e.g., *An. tenebrosus*, *An. samarensis*, *An. argyropus*, *An. campestris*, *An. donaldi*, *An. umbrosus*, *An. letifer*, and *An. roperi*) have this spot between sc-r and r_1-r_s . It seems to be in a position between the two crossveins in species with an overall darkening of the wing and is small or completely missing in some (e.g., *An. perplexens*, *An. punctipennis*, *An. grabhamii*, *An. collessi*, and *An. wellingtonianus*). An apparent exception is *An. gigas* (sensu lato). Here, wing coloration is not reduced, but this spot is missing. *Anopheles pseudopunctipennis* and *An. franciscanus* are unique because this spot, although just distad of sc-r as in other species, is also clearly situated on r_1-r_s . By the definition given below, this would be an accessory sector pale spot or a combination of the sector pale and accessory sector pale spots. We assume that this spot in species of the subgenus *Anopheles* is the sector pale as it is in species of the other subgenera. It may be of independent origin and homoplasious to the sector pale of the other subgenera.

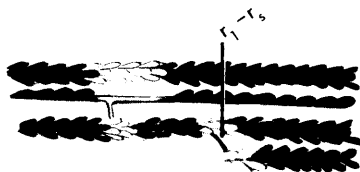
The second crossvein examined connects radius-one and the radial sector (r_1-r_s) (Fig. 1–6, 7–24,

middle arrow; 25–27). It often has been depicted as a gently curved R_s connected to R_1 . We believe it is a crossvein because in most anophelines we examined, it usually appears as a distinct vertical vein between R_1 and R_s . Vein R_s usually has an extension of varying lengths (called a spur by some) proximal to this crossvein (Fig. 25 and 26). We found variations ranging from no apparent proximal extension of R_s to a long extension with scales (Fig. 25–27). The only specimens seen that had the curved connection to R_1 , often depicted in illustrations, were among species of the subgenus *Cellia* (e.g., *An. kochi*, *An. kolambuganensis*, *An. koliensis*, *An. dirus*, *An. balabacensis*, *An. cristatus*, *An. pujutensis*, *An. macarthuri*, *An. riparis*, *An. sulawesi*, *An. leucosphyrus*, *An. takasagoensis*, and *An. introlatus*). But even among these few species some specimens had one side with a curved r_1-r_s and the other had a vertical vein and a small extension. The r_1-r_s crossvein most commonly is called the radial crossvein or the marginal crossvein (Table 2). We found that in all species examined belonging to the subgenera *Cellia*, *Nyssorhynchus*, *Kerteszia*, and *Lophopodomys*, the r_1-r_s crossvein corresponds to the position of the accessory sector pale spot. This association also was noted by Christophers (1913) (accessory sector nodal point). We redefine the **accessory sector pale spot** as the group of pale scales associated with crossvein r_1-r_s on vein R_s , sometimes also on veins Sc and C , usually separated by a dark spot from the sector pale but sometimes fused with the sector pale.

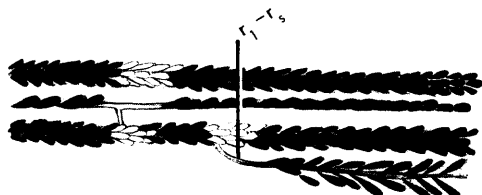
In species of the subgenus *Anopheles*, including the Arribalzagia Series (Fig. 2 and 6), the accessory sector pale spot is absent (however, see discussion of *An. pseudopunctipennis* and *An. franciscanus* above). Because a dark spot divides the sector pale spot into two pale areas in species of the Arribalzagia Series, there could be confusion that the most distal pale spot is the accessory sector pale. Since



25 *An. (Nyssorhynchus) albimanus*



26 *An. (Cellia) hackeri*



27 *An. (Cellia) hackeri*

Fig. 25-27. Wings of female anophelines (see text for abbreviations). (25) *An. (Nyssorhynchus) albimanus*, Costa Rica, CR 438, (26) *An. (Cellia) hackeri*, Thailand, Khau Lau, 00439-1, 8.47.R., (27) *An. (Cellia) hackeri*, Thailand, Khau Lau, 00439-101, 8.47.R.

there is no association of the pale spot with r_1-r_5 , we conclude that the accessory sector pale spot is absent in the Arribalzagia Series. The sector pale spot, but not the accessory sector pale, exists in species of the series. The dark spot usually present in the sector pale is unique to this group. We name this the **accessory sector dark spot** (Fig. 2).

Preapical Pale and Apical Pale Spots. A third area on the wings of species of the Arribalzagia Series which does not conform to the generalized genus *Anopheles* wing is the area beyond the preapical dark. In species of the subgenus *Cellia*, the preapical dark spot is followed by the preapical pale, the apical dark, and (most distal) the apical pale. Harbach & Knight (1980) define all of the apical costal spots in relation to each other. The preapical pale is "the group of pale scales occurring between the preapical dark and apical dark on the costa and radius-one." The apical dark is "the group of dark scales on the costa and proximad of the apical pale." The apical pale is "the group of pale scales

usually occurring at the extreme apex of the wing distad of the apical dark on the costa and radius-one; sometimes absent." In anophelines other than the subgenus *Cellia*, these definitions are not adequate to name the spots because one of the pale spots may be absent. Without morphological markers, it is difficult to determine which spots are present and which are absent. We assume that the spots are homologous and propose definitions which serve to name these spots in all species of the subgenus *Anopheles* and other spotted-wing mosquitoes.

In species of the subgenus *Cellia*, the preapical and apical pale spots usually are present, so it is not difficult to distinguish them (Fig. 1). Note that the end of vein R_1 is pale-scaled and ends at the apical pale spot. Christophers (1933) noted that the apical pale spot clearly is identifiable at the end of R_1 at the apex of the wing; beyond the end of R_1 is the scale-thickened wing margin which merges into the fringe and is referred to as the wing apex. In his key for the subgenus *Nyssorhynchus*, Christophers (1933, 98) states that the pale spot is not at the end of R_1 but basal to it, which is consistent with our definition of the preapical pale spot. Gater (1935) also saw pale scales at the end of R_1 , which he called the apical pale area. Harrison & Scanlon (1975) recognized the difficulty of defining the apical and preapical pale spots in the subgenus *Anopheles* but did so by defining the preapical pale as those pale scales proximal to the tip of R_1 . We agree with this interpretation except for their (admitted) arbitrary naming of the spot in species of the Umbrosus Group. We think that members of the Umbrosus Group have apical pale spots and not preapical pale spots.

The scales at the end of R_1 become the basis for our definition of these two pale spots. We define the **apical pale spot** as the area of pale scales on the costa at the end of R_1 . Note that pale scales also are usually (but not always) present on the end of R_1 . We define the **preapical pale spot** as those pale scales on the costa and radius-one proximal to the end of R_1 , between the preapical dark and apical dark. We define the **apical dark spot** as the area of dark scales at or proximal to the end of R_1 and distal to the preapical pale (note that when the apical dark is at R_1 , there is no apical pale spot [Fig. 2-6]).

The color of the scales on the costa at the end of R_1 are critical when deciding if an apical pale or preapical pale is present. In most cases it is clear that R_1 ends or does not end in pale scales, but some species are more difficult to interpret. *An. parapunctipennis* (Fig. 35) has a preapical pale but no apical pale, and even though there are pale scales far out on the apex of the wing, there are a couple of dark scales at the end of R_1 , and the fringe at the end of R_1 is dark. In *An. hectoris* (Fig. 31), both pale spots are present, but the apical pale is represented by one or two pale scales at the end of R_1 and by a pale fringe. Some species of the subgenus *Anopheles* are illustrated (Fig. 28-35)

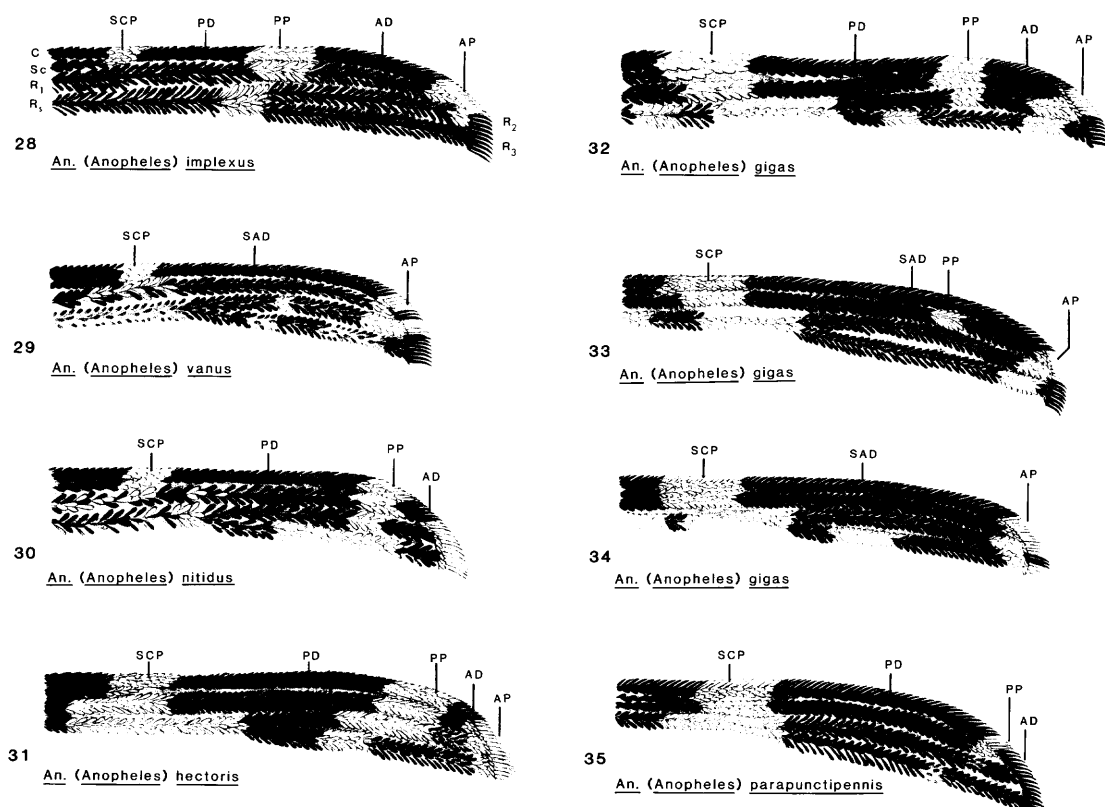


Fig. 28-35. Wings of female anophelines (see text for abbreviations). (28) *An. (Anopheles) implexus*, Belgian Congo, Elisabethville, (29) *An. (Anopheles) vanus*, Philippine Islands, Tawi Tawi, 8-233, (30) *An. (Anopheles) nitidus*, Vietnam, Phu Lam, PL 2994, (31) *An. (Anopheles) hectoris*, Guatemala City, 23-V-49, (32) *An. (Anopheles) gigas*, Ledo Assam, V.I. Miles-44, (33) *An. (Anopheles) gigas*, Ledo, Assam, 18th MSU, (34) *An. (Anopheles) gigas*, Ledo, Assam, V.I. Miles-44, (35) *An. (Anopheles) parapunctipennis*, Guatemala, Esquipulas.

which show the contrast between the positions of the apical and preapical pale spots. In *An. implexus* (Fig. 28) and *An. hectoris* (Fig. 31), both spots are present; in *An. vanus* (Fig. 29), only the apical pale is present; and in *An. nitidus* (Fig. 30) and *An. parapunctipennis* (Fig. 35), only the preapical pale is present. Three forms of *An. gigas* from the same locality (Fig. 32-34) all have an apical pale, but one (Fig. 32), shows the presence of a preapical pale, another has the preapical pale present only on R_1 , and a third lacks a preapical pale. Because the absence of the presector pale produces a dark spot (humeral dark and presector dark combined), the **subbasal dark spot** (Fig. 4, 5, and 37), it also is useful to name the dark spot distal to the subcostal pale when the preapical pale is not present. We propose the term **subapical dark spot** (Fig. 29, 33-34, and 37).

By these definitions, all members of the Arribalzaga Series (Fig. 7-24) (except *An. mattogrossensis*, which has an apical pale), have only a preapical pale spot. The preapical pale in most species of the Arribalzaga Series have an extra dark area not found in other anophelines. We designate this the **accessory preapical dark spot** (Fig. 2). A few

species (*An. shannoni*, *An. mattogrossensis*, and probably *An. bustamentei*), lack this accessory dark spot. Among the other species, the size and darkness of this spot and the size of the preapical pale could be useful as species characters. For example, the accessory preapical dark in *An. rachoui* is weak (Fig. 10), and in *An. guarao*, *An. peryassui*, and others, it is small. In two species (*An. minor* and *An. shannoni*), the most distal edge of the preapical pale ends at R_1 . Without careful observation, the dark scales at the end of R_1 could be overlooked. In the few specimens of two other species (*An. fluminensis* and *An. guarao*), R_1 usually ends in pale scales. Strictly speaking, this contradicts the definition of the preapical pale given above and this pale spot then would be considered an apical pale. Further study is needed to define precisely the spots occurring distal to the subcostal area in these few species of the Arribalzaga Series.

The wings of species of the subgenera *Nyssorhynchus* (Fig. 3), *Kerteszia* (Fig. 4), and *Lophopodomyia* (Fig. 5) are dark at the end of R_1 and therefore have an apical dark spot but lack an apical pale spot. In species of the subgenus *Anopheles*, there is correspondence between the presence

and absence of these spots and the present classification (Reid & Knight 1961).

The appendix is modified from Reid & Knight (1961). Species have been added, and species with unicolorous wings have been omitted. The single species in the Christya Series (*An. implexus*), has both an apical pale and preapical pale spot. It is unique in that it has speckled legs similar to those of most species of the Arribalzagia Series; prominent abdominal scale tufts (smaller tufts are found in species of the Arribalzagia Series), and pale hindtarsomeres like members of the subgenus *Nyssorhynchus*. These characteristics all suggest that it is a possible ancestor of the New World species of the subgenera *Nyssorhynchus*, *Kerteszia*, *Lophopodomyia*, and the Arribalzagia Series.

Among the Myzorhynchus Series, all species have either a preapical pale or an apical pale. An apical pale is found in species of the Albotaeniatus, Bancroftii, Barbirostris, and Umbrosus Groups. A preapical pale is found in species of the Coustani and Hyrcanus Groups. Some specimens of *An. stnensis* in the Hyrcanus Group exhibit a borderline condition in which there may be a few pale scales on the fringe at the end of R_1 , suggesting an apical pale spot.

In the Angusticorn Section, species of the Cyclolepteron and Lophoscelomyia Series have apical pale spots. In the Anopheles Series, species of the Punctipennis Group and the Plumbeus Group have apical pale spots, as do species of the Lindesayi Group (except for *An. gigas*, which may have a preapical pale spot). A single species in the Maculipennis Group (*An. occidentalis*) has an apical pale spot. The Pseudopunctipennis Group seems to be a mixture of unrelated species because it includes species with both apical pale and preapical pale spots.

Humeral Pale Spot. The humeral pale spot is the only spot defined by Harbach & Knight (1980) in relation to a fixed reference point. It is defined as "the group of pale scales occurring at or slightly distal to the humeral crossvein on the costa." Most anophelines with costal spots exhibit the humeral pale spot.

Further Observations on the Subgenera of Anopheles. *Kerteszia* (Fig. 4). Species of the subgenus *Kerteszia* have all the spots found in species of the subgenus *Cellia* except a prehumeral pale, presector pale, and apical pale. The large dark spot produced by a missing presector pale is called a subbasal dark by Harbach & Knight (1980). As discussed above, in the subgenus *Kerteszia* the subcostal vein meets the costa at the base of the subcostal pale spot or in the sector dark spot. We found that the humeral dark of Zavortink (1973) is the subbasal dark of Harbach & Knight (1980) and that his presectoral dark and sectoral dark, with an intervening sectoral pale, is our sector dark interrupted by the accessory sector pale. Species of the subgenus *Kerteszia* also have an apical dark but no apical pale. In this subgenus, it appears that the

distance between $sc-r$ and r_1-r_2 is relatively greater than in any other group, but no measurements were taken as part of this study.

Nyssorhynchus (Fig. 3). Species with the most spots lack only the basal dark and the apical pale. Our interpretation differs from that of Faran (1980) (Table 1). We consider his subbasal dark and pale to be the humeral dark and presector pale, his presector pale to be the sector pale, his sector pale to be the accessory sector pale, and his subcostal dark to be the sector dark (in part).

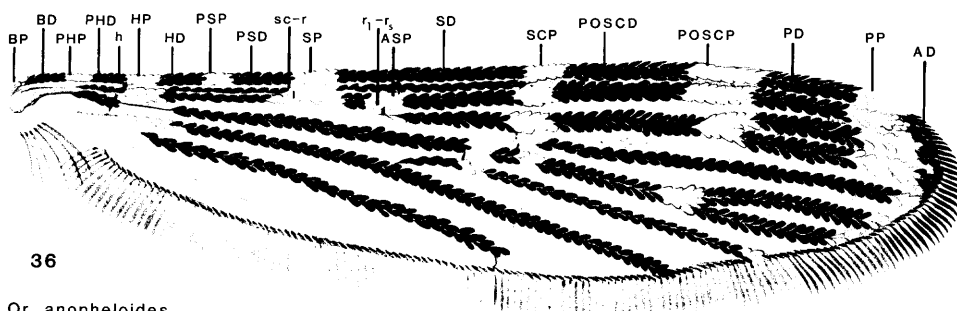
Lophopodomyia (Fig. 5). Species of the subgenus *Lophopodomyia* with the full complement of spots apparently lack an apical pale and probably a basal pale. The few species we have seen have a combined accessory sector pale and sector pale except for the species illustrated (*An. gilesi*), which has a dark interruption between these two spots on R. In the species without dark scales between these two spots, there is some resemblance to *An. (Anopheles) pseudopunctipennis*.

Anopheles (Fig. 6). Species of this subgenus have the most reduced costal spotting of all anophelines. The species illustrated (*An. nitidus*), is typical. The basal pale and prehumeral pale are missing, the presector pale may be present, but the scattering of pale scales obscures interpretation. The sector pale is present only on R. As discussed above, there is no accessory sector pale. This species has an apical dark but no apical pale.

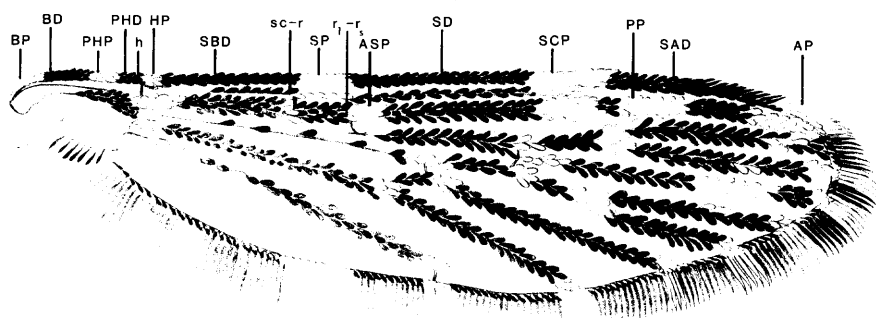
Observations on Other Culicidae. Although the argument for or against homoplasy of spots in the genus *Anopheles* is not resolved, our definitions of the spots using morphological markers allow them to be used in descriptions and keys. It was interesting to find many of these same spots, usually at the same positions, in species of other genera. We apply the same names used for spots in the genus *Anopheles* to other Culicidae to give some stability to the system of nomenclature. We did not examine all of the nonanopheline species known to have pale and dark spots or speckling on the wing. We are aware of a few additional species not listed here, particularly in the genera *Aedes* and *Uranotaenia*, but feel they would add little and are secondary to our original objective of naming costal wing spots in anophelines.

Orthopodomyia (Fig. 36). The genus *Orthopodomyia* have spots readily comparable with the spots in *Anopheles (Cellia)*. The position of these spots in relation to the humeral crossvein, $sc-r$, r_1-r_2 , the end of the subcosta, and the end of R_1 is consistent with the definitions given here. The only exception is in the subcostal area which resembles the subcostal area in species of the Arribalzagia Series which have a subcostal pale, postsubcostal dark, and postsubcostal pale. The postsubcostal pale is at the level of the furcation of veins R_2 and R_3 as in the Arribalzagia Series.

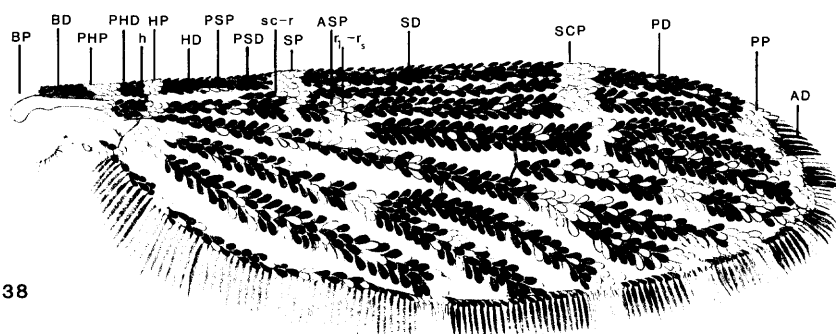
Aedes (Finlaya) Kochi Group (Fig. 37). Belkin (1962) based his terminology of wing spots on this taxon. Species of this group exhibit spots at the



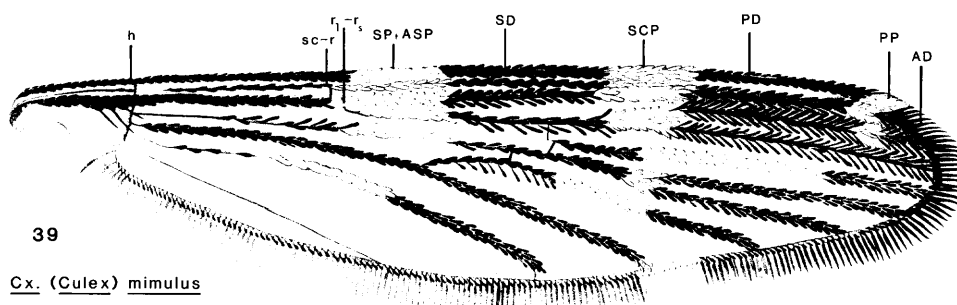
36
Or. anopheloides



37
Ae. (Finlaya) bougainvillensis



38
Ad. (Aedeomyia) catasticta



39
Cx. (Culex) mimulus

Fig. 36-39. Wings of female mosquitoes (see text for abbreviations). (36) *Or. anopheloides*, Ryukyu Islands, Iriomote Island, Itokawa-rindo, K-0571-11, (37) *Ae. (Finlaya) bougainvillensis*, Solomon Islands, Bougainville Island, 27 June 1944, (38) *Ad. catasticta*, Phillipine Islands, Samar, (39) *Cx. (Culex) mimulus*, New Guinea, APO 713-1, VII-3-44.

same positions as *Anopheles* (*Cellia*) with relation to the humeral crossvein, $sc-r$, r_1-r_s , the end of the subcosta, and the end of R_1 . The only exception is the apparent absence of a presector pale. The resultant dark spot is the subbasal dark spot. In the species illustrated (*Ae. bougainvillensis*), the preapical pale does not continue to the costa. Belkin's accessory subcostal pale area is the preapical pale and his median dark is the sector dark; otherwise his terminology is the same as used here.

Aedeomyia (Fig. 38). The illustrated species (*Ad. catasticta*), has the full complement of spots, although the pale spots are either yellow or white. In all species, the following spots are white-scaled: basal pale, humeral pale, sector pale, accessory sector pale, subcostal pale, and preapical pale.

Culex (Fig. 39). A number of *Culex* (*Culex*) and *Culex* (*Lutzia*) have three main costal pale spots which were designated "1," "2," and "3" by Sirivanakarn (1976). Some of these spots are of good diagnostic value for several species (Matsuo et al. 1974). Although there is not as good a correspondence in the pattern of spots here as with the other nonanopheline genera, there is enough to make use of our proposed definitions. The first pale spot is usually within the area of $sc-r$ and r_1-r_s crossveins, thus corresponding to a spot made up of the sector pale and accessory sector pale. The r_1-r_s crossvein is curved into R_1 as described for some species of *An.* (*Cellia*). The next pale spot is at the end of the subcostal vein and is therefore the subcostal pale spot. The third pale spot is found proximal to the end of R_1 and is therefore the preapical pale spot.

Psorophora (*Grabhamia*) (not illustrated). The single species examined (*Ps. signipennis*), has no regular spots on the basal half of the wing, but spots are present that correspond to the subcostal pale, preapical dark, preapical pale, apical dark, and apical pale.

Uranotaenia (*Uranotaenia*) (not illustrated). The three species examined have spots corresponding to the subcostal pale, subapical dark, and apical pale.

Summary and Conclusions

Review of the literature and examination of numerous mosquito species bring us to the following primary conclusions regarding nomenclature of the costal spots on spotted-wing species in the genus *Anopheles* and spotted-wing culicines:

- Anophelines in the Arribalzagia Series are the only culicids with the subcosta ending in an isolated dark spot distal to the sector dark spot. This character reinforces the hypothesis that the Arribalzagia Series is monophyletic.
- *Anopheles* (*Anopheles*) species, including the Arribalzagia Series, have no accessory sector pale spot.

- Species of the Arribalzagia Series have three unique areas of costal wing spotting: the sector pale spot has an accessory sector dark spot; the subcostal area is made up of pre- and postsubcostal pale and dark spots on either side of the subcostal dark spot; and the preapical pale spot has an accessory preapical dark spot.
- The sector pale and accessory sector pale spots are redefined in relation to the $sc-r$ and r_1-r_s crossveins, respectively, and the preapical and apical pale spots are redefined in relation to the end of R_1 .
- The presence or absence of the preapical and apical pale spots in species of the subgenus *Anopheles* usually is consistent with present concepts of classification within the subgenus.
- The names of wing spots derived from definitions given here for species of the genus *Anopheles* usually can be applied to species of the genera *Aedes*, *Aedeomyia*, *Culex*, *Orthopodomyia*, *Psorophora*, and *Uranotaenia*.

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Appendix

Classification system of wing spots of *Anopheles* (*Anopheles*) based on Reid & Knight (1961) (species with unicolorous wings belonging to these series and groups are not included). a, apical pale spot present; p, preapical pale spot present; —, the species was not examined.

Laticorn Section

Christya Series

a, p *implexus*

Arribalzagia Series

p *anchietai*
p *apicimacula*
p *bonnei*
p *bustamentei*
p *evandroi*
p *fluminensis*
p *gabaldoni*
p *guarao*
p *intermedius*
p *maculipes*
p *malefactor*
a *mattogrossensis*
p *mediopunctatus*
p *minor*
p *neomaculipalpus*
p *perysui*
p *pseudomaculipes*
p *punctimacula*
p *rachoui*
p *shannoni*
p *veruslanei*
p *vestitipennis*

Myzorhynchus Series

— *africanus*
— *koreicus*
a *obscurus*
(Albotaeniatus Group)
a *albotaeniatus*
— *balerensis*
— *ejectoi*
a *montanus*
a *saperoi*
a *saperoi ohamai*
(Bancroftii Group)
a *bancroftii*
— *b. var. barbiventris*
a *pseudobarbiventr*

(Barbirostris Group)

- a *barbirostris*
- a *barbumbrosus*
- a *campestris*
- a *donaldi*
- a *franciscoi*
- a *hodgkini*
- a *manalangi*
- a *pollicaris*
- a *reidi*
- a *vanus*

(Coustani Group)

- p *coustani*
- *caliginosis*
- p *fuscicolor*
- p *namibiensis*
- p *paludis*
- p *symesi*
- p *tenebrosus*
- p *ziemanni*

(Hyrceanus Group)

- p *argyropus*
- *chodukini*
- p *crawfordi*
- p *hyrcanus*
- *kweiyangensis*
- p *lesteri*
- p *nigerrimus*
- p *nitidus*
- p *peditaeniatus*
- *pseudosinensis*
- p *pullus*
- p *sinensis*
- p *sineroides*
- p *pursati*
- p *yatsushiroensis*

(Umbrosus Group)

- a *baezai*
- a *brevirostris*
- a *collessi*
- *hunteri*

- a *letifer*
- a *roperi*
- a *samarensis*
- a *separatus*
- *similissimus*
- a *umbrosus*
- a *whartoni*

Angusticorn Section

Cyclolepteron Series

- *annulipalpis*
- a *grabhamii*

Lophoscelomyia Series

- *annandalei*
- a *asiaticus*
- a *interruptus*
- a *noniae*

Anopheles Series

(Lindesayi Group)

- a, p *gigas*
- a *lindesayi*
- a *wellingtonianus*

(Maculipennis Group)

- a *occidentalis*

(Plumbeus Group)

- a *xelajuensis*
- a *powderi*
- a *arboricola*
- a *fausti*

(Pseudopunctipennis Group)

- p *eiseni*
- a *franciscanus*
- a, p *hectoris*
- p *parapunctipennis*
- a *pseudopunctipennis*
- *tibiamaculatus*

(Punctipennis Group)

- a *bradleyi*
- a *crucians*
- a *georgianus*
- a *perplexens*
- a *punctipennis*